

EVIDENCE FOR DISPARITY DETECTING NEURONES IN THE HUMAN VISUAL SYSTEM

BY COLIN BLAKEMORE AND BRIAN HAGUE

From the Physiological Laboratory, University of Cambridge,

Cambridge CB2 3EG and the Psychological Laboratory,

University of Cambridge, Cambridge CB2 3EB

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SUMMARY

1. It is known that adaptation to a grating pattern causes a rise in the contrast threshold for test gratings of similar spatial frequency and orientation.

2. We find this after-effect also to be disparity-specific. Adaptation to a grating at zero horizontal disparity (at the same distance as the fixation point) causes a greater elevation of threshold for patterns at the same disparity than for those at nearby disparities, closer or more distant than the fixation point.

3. Adaptation to a grating at some disparity other than zero causes a disparity-specific elevation of threshold centred on the adapting disparity.

4. This finding also applies if the observer adapts to a grating but single bright bars are used as the test stimuli.

5. The disparity-specific 'tuning curves' revealed by these techniques are quite broad, having a half-width at half-amplitude of several min of disparity.

6. Adaptation to a grating at one disparity causes an apparent change in the distance of test gratings at nearby disparities.

7. We compare these psychophysical experiments with the properties of disparity-selective binocular neurones in the visual cortex of cats and monkeys.

INTRODUCTION

We can do amazing things with the tiny distorted images that fall on our constantly moving eyes, but stereopsis is surely one of the pinnacles of human visual resolution. If it is surprising that we can distinguish a vernier shift of less than 10 sec of arc in a long straight line seen by one eye, how much more unexpected it is that we can judge the relative positions of images in the two eyes to about the same accuracy (Berry, 1948). Only

recently has there been any hint of how the brain achieves this remarkable performance.

The vast majority of neurones in the visual cortex of the cat and monkey are stimulated by a line-shaped target or edge shown to either eye, or better still to both (Hubel & Wiesel, 1962, 1968; Barlow, Blakemore & Pettigrew, 1967; Pettigrew, Nikara & Bishop, 1968; Noda, Creutzfeldt & Freeman, 1971). This could be the means by which the brain identifies the two images of a single object, one in each eye. There is considerable irregularity in the lay-out of the receptive fields: binocular cells all with their input from a particular place on one retina can have their receptive fields in a wide range of different positions on the other retina. So, from cell to cell, the horizontal retinal disparity differs enormously, over several degrees (Barlow *et al.* 1967; Nikara, Bishop & Pettigrew, 1968; Blakemore, 1970*a*; Hubel & Wiesel, 1970; Joshua & Bishop, 1970). To get the very best response out of a cortical neurone, an object of the appropriate orientation must lie in the correct three-dimensional position in space, so that its image falls on the receptive field in both eyes. The tuning of these binocular cells for the disparity of the stimulus can be very precise, so that if the disparity is altered by only a few min of arc from the optimum, the cell's response may be completely occluded. Different cells have different optimal disparities and hence they respond to objects at different distances from the eyes.

In order to press further the analogy between binocular neurones in animals and human binocular vision it would be gratifying to see some evidence for disparity-selective neural mechanisms in man. Recently, several investigators have measured the way in which the human visual system adapts to specific sensory stimuli. For instance, if you look at a pattern of dark and light stripes it seems to fade gradually, the apparent contrast becoming lower and lower (Blakemore, Muncey & Ridley, 1971). After exposure to such a high-contrast pattern you would find that your threshold contrast for the detection of the stripes in a test grating is markedly raised; but this is only true if the adapting and test gratings are similar in orientation (Gilinsky, 1968; Sekuler, Rubin & Cushman, 1968; Blakemore & Campbell, 1969*a*; Blakemore & Nachmias, 1971) and in spatial frequency or bar-width (Pantle & Sekuler, 1968; Blakemore & Campbell, 1969*a, b*).

All this has been taken to mean that staring at a grating desensitizes a subset of visual neurones specifically tuned to the orientation and width of the stripes (Blakemore & Campbell, 1969*b*). The fact that, after adapting in one eye, the after-effect transfers to the other, makes a comparison with binocular, orientation-specific cortical neurones very attractive.

Cortical neurones are disparity-specific – they respond best only if the

image is correctly positioned in both eyes – so it occurred to us that the after-effect of adaptation to a grating might also be sensitive to the disparity of the adapting grating. We have adapted to gratings at a particular distance (and thus at a certain retinal disparity) and afterwards measured the contrast threshold for gratings at different disparities. In this way we have been able to confirm that there are disparity-selective mechanisms in the human brain.

Definitions

Spatial frequency: number of cycles of a grating per degree of visual angle.

Spatial period: angular width of a single cycle of a grating.

Contrast of a grating: $I_{\max} - I_{\min} / I_{\max} + I_{\min}$, where I_{\max} , I_{\min} are the maximum and minimum luminances in the grating.

Contrast of a bright bar: $I_{\max} - I_{\text{back}} / 2 \cdot I_{\text{back}}$, where I_{back} is the luminance of the background.

METHODS

An observer sat in a darkened room and looked straight ahead at a large display oscilloscope screen (Hewlett Packard 1300A), 228 cm from his eyes. The screen was masked down to a rectangular area 24 cm wide and 18 cm high so that it subtended 6 deg by 4.5 deg at the subject's eyes. He also saw two other small oscilloscope screens optically superimposed on the display oscilloscope by means of half-silvered mirrors: Fig. 1 shows the arrangement of the apparatus. All three screens were optically at exactly the same distance and all had green-yellow (P-31) phosphors. Polaroid filters in front of the subject's eyes and in the optical pathway from the two small oscilloscopes allowed him to see only one of them with each eye: the display oscilloscope was seen by both.

We used the television technique of Schade (1956), with Campbell & Green's refinements (1965) to produce vertical gratings, or a single vertical bright bar, on the display oscilloscope. A uniform raster filled the screen with light and the patterns were generated by applying signals from a function generator (locked in synchrony with the time-base repetition frequency) to the intensity modulation. The gratings and single bar could be turned on and off and their contrast varied without altering the mean luminance, or background luminance, on the screen, which was about 10 cd.m⁻². The diffuse surround luminance was about 0.5 cd.m⁻².

On each small screen we applied a signal with a high-frequency triangular wave form on the vertical amplifier to generate a single thin bright vertical line, 1.5 deg long and 1.5 min wide, with a luminance at the eye of 10 cd.m⁻², against a dark background. The horizontal position of this line could be driven externally by applying to the horizontal amplifier a low-frequency signal with a triangular wave form (so that the vertical line drifted from side to side) or a steady d.c. voltage (so that it rested at some position away from the centre of the screen). The signals applied to the two small screens were always identical except that the steady d.c. voltage was electronically inverted for one of the screens, so the horizontal displacement of the line was in opposite directions on the two screens.

Adaptation conditions. During adaptation a high-contrast grating, with a sinusoidal intensity profile, appeared on the display oscilloscope. The small line was usually set exactly in the centre of each small screen and the two were driven in synchrony from side to side by the triangular signal. So the observer saw a *single* binocularly fused bright line moving back and forth in the exact plane of the grating. He used the line as a fixation target, letting his gaze drift from side to side. In this

way we avoided the formation of a conventional negative after-image of the grating. The amplitude of the drift was equal to 2.5 periods of the grating, moving the fixation line from the centre of a bright bar to the middle of a dark one, and back again; the frequency of the triangular horizontal deflexion was about 0.25 Hz.

Test conditions. At the flick of a switch the experimenter could change the entire display to a new configuration. The adapting grating on the display oscilloscope was replaced by a low-contrast sine-wave grating of the same spatial frequency, or by a single bar, and the contrast of this pattern was under the control of a logarithmic potentiometer that the subject held. He adjusted the contrast until he could just distinguish the test pattern (which was being turned on and off at 1.5 Hz) and pressed a button to print out the setting. At the same time the fixation lines were changed: the triangular signal was switched to a steady d.c. voltage of opposite polarity for the two screens, thus displacing the lines sideways in opposite directions in the two eyes. Hence the fixation line was now at some horizontal disparity (equal to the sum of the displacement in the two eyes) relative to the original plane of the adapting pattern. So when the switch was thrown the fixation line suddenly stopped moving from side to side and jumped forwards or backwards in depth to some fixed position. The d.c. voltage controlling the disparity was set by the experimenter on a multi-turn potentiometer and monitored on a digital voltmeter. The adapting situation could be restored as easily as it was removed.

Problems. We required the observer to fixate the small line all the time, converging or diverging his eyes when we changed from adapting to test situations. So he had to set his contrast threshold for a pattern that he was not fixating binocularly (see Fig. 1). Admittedly, this is not an easy task and the subject required some training to maintain constant convergence. Consequently, most of our experiments were performed on the first author (C.B.) who has had considerable training in psychophysical observation. The main results, however, were all confirmed on a second observer (D.T.) who, although an experienced subject, was naïve as to the precise nature of the experiment.

Stability of gaze was not the only possible cause of error: any d.c. drift or change in gain for the horizontal deflexion of the fixation lines would have upset the experiment. We checked at the end of each session that the gain was still correctly calibrated, and the observer was constantly able to monitor any d.c. drift by reporting if the fixation line deviated in depth from the plane of the grating during the adapting condition. Only very rarely, during particularly long sessions, did any d.c. error occur and then we terminated the experiment immediately.

RESULTS

The logic of our experiment should now be clear. We asked the subject to hold his gaze fixedly on the bright line, during adapting and test conditions, so that the adapting pattern was usually at zero disparity, in the same plane as fixation. But, in the test situation, when the fixation line changed in depth and the subject re-converged his eyes, the screen of the display oscilloscope was set to some new retinal disparity, relative to the fixation point. If the fixation point came forward, by shifting, say, 10 min to the left in the right eye and 10 min to the right in the left eye, then when the subject fixated the line the large screen was at an absolute *divergent* (uncrossed) disparity of 20 min. If the fixation line was shifted backwards the display screen was at an absolute *convergent* (crossed)

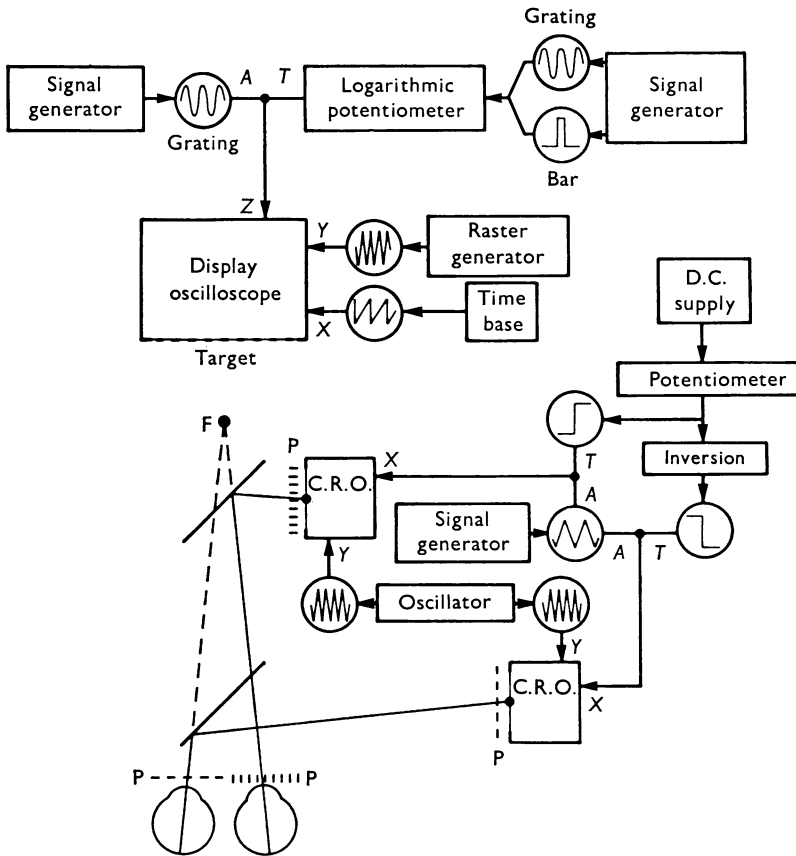


Fig. 1. A schematic diagram of the apparatus, showing the target generated on the large display oscilloscope and the fixation lines on the two smaller oscilloscopes (labelled C.R.O.). The sources of the signals for the horizontal (X), vertical (Y) and intensity (Z) axes of the oscilloscopes are shown, with the wave forms of the signals in the circular insets. Switching points, marked A and T , in the circuits indicate alternative signals for adapting and test conditions respectively. The fixation line, F , was composed of the fused images of the individual lines on the small oscilloscopes, since polaroid filters (P) over the eyes and the two screens permitted only one screen to be seen by each eye.

So during adaptation a sinusoidal grating appeared on the display oscilloscope, seen by both eyes through the half-silvered mirrors, and the fixation line moved from side to side with triangular wave form in a fronto-parallel plane (usually the same plane as the grating). During test conditions a d.c. voltage displaced the fixation line to some new disparity while a flashing grating or bar, whose contrast the subject could regulate with a logarithmic potentiometer, appeared on the display oscilloscope.

disparity. (Blakemore, 1969, discusses the terminology and sign conventions for retinal disparity.) We measured the change in contrast threshold after adaptation as a function of the relative disparity of adapting and test patterns.

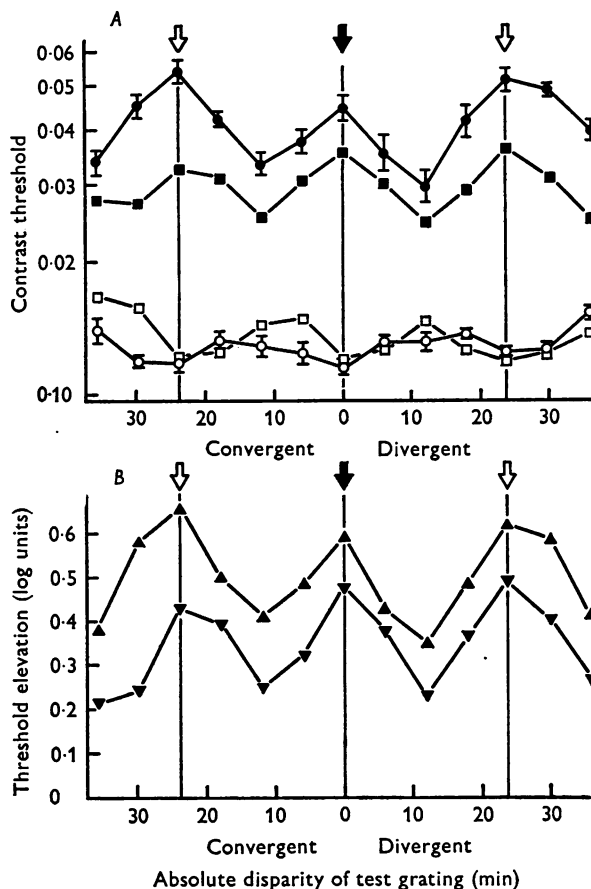


Fig. 2. *A*. Contrast threshold for a grating of 2.5 c/deg as a function of its retinal disparity before (open symbols) and after (filled symbols) adapting to a grating of the same frequency, and a contrast of 0.7, at the fixation point (zero disparity, marked with a filled arrow). The open arrows show the disparities equal to the spatial period of the grating, at which it came back into phase on the two retinae and thus appeared again to be in the same plane as the fixation point. (○ and ●: means of $N = 8$ for subject C.B., with their standard errors. □ and ■: means of $N = 6$ for subject D.T.) *B*. Difference curves for the two subjects (▲ for C.B., ▼ for D.T.) from Fig. 2*A*.

Adapting to gratings: testing with gratings

First we performed a control experiment in which the observer repeatedly set a test grating, turning on and off at 1.5 Hz, to threshold, with no prior adaptation. In between settings the display screen went blank, except for the uniform raster. The experimenter varied the disparity of the fixation line in a regular series, taking two or three readings at each disparity, over the range from convergent to divergent, then two or three more settings at each, on the way back through the series. The open symbols in Fig. 2A, circles for one subject, squares for the other, show the results of the unadapted experiment, using a grating with a spatial frequency of 2.5 c/deg (cycles per degree of visual angle). Clearly there is a small but significant variation of threshold with the disparity of the grating.

Consider how and why the threshold contrast varies with disparity: it is a cyclical function with the lowest thresholds at 0 (marked with a filled arrow), +24, and -24 min disparity (marked with open arrows). Remember that the spatial period of a 2.5 c/deg grating is 24 min. So when the eyes converge or diverge by a combined angle of that magnitude then such a pattern will re-establish exactly the same relative phase relationships on the two retinae – in other words the grating will again be fixated. The perceptual correlate of this is that, as the eyes are gradually converged, the grating keeps 'locking in' at the plane of the fixation point for every 24 min of convergence. So at the disparities indicated by the open arrows and vertical lines of Fig. 2 the subject was in fact fixating the grating and its actual disparity was again zero. It is of some interest that the threshold varies at all with disparity. If the detection process were completely independent in the two eyes and the final likelihood of resolving a pattern were to be based on simple probability summation, as suggested for instance by Pirenne (1943), then the relative position of the eyes should be of little consequence. Likewise, if signals from the two eyes, plus uncorrelated noise, just summate before the threshold device, which is the simplest version of Campbell & Green's hypothesis (1965), the binocular threshold for a grating should again be independent of the exact location of the patterns on the two retinae. The mere fact that it is not suggests that the final threshold device resides after a binocular combination site whose output is influenced by the disparity or relative phase of the patterns.

Now we repeated the experiment but before taking any threshold readings the subject adapted constantly to a grating of 2.5 c/deg at a contrast of 0.7 for 3 min (Blakemore & Campbell, 1969*b*, showed that this period of time allows the after-effect to build up to its maximum value). All the time the fixation line was moving back and forth exactly in the

plane of the grating, so the pattern was at zero disparity. Then we switched to the test situation, the fixation line jumping to some new depth and the grating changing to the flashing, low-contrast version whose contrast was under the subject's control. He made a setting of threshold in a second or two, pressed a button to print out the result, and the adapting display was restored for 15 sec to allow the adaptation to build up again. The experimenter changed the disparity between groups of settings, as before.

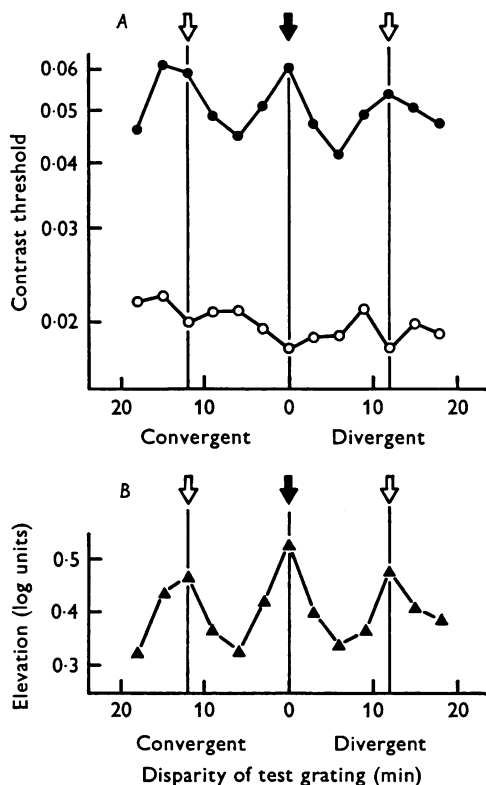


Fig. 3. This Figure illustrates an identical experiment to that described by Fig. 2, but a 5 c/deg grating was used throughout. Subject C.B.; $N = 4$.

The filled symbols in Fig. 2A plot the new threshold, as a function of disparity, during adaptation. When the test grating is being fixated (at disparities of 0, +24 and -24 min) the threshold is markedly elevated: when it is completely out of phase on the two retinæ (at disparities of ± 12 and ± 36 min) the threshold is much lower. These differences are highly significant, especially when they are treated in terms of elevation of threshold, because the natural variations in unadapted threshold are opposite in direction. Fig. 2B plots the increase in threshold for the two subjects.

One subject shows a rather stronger over-all after-effect than the other, but the basic shapes are very similar.

The whole experiment was repeated for one of the subjects, using adapting and test gratings of 5 c/deg, and Fig. 3 shows the outcome. The co-ordinates are identical to those of Fig. 2 but the range of disparity covered is smaller. The arrows again mark the disparities at which the grating was in phase on the retinae and, since the spatial frequency was 5 c/deg, only 12 min of disparity were needed for zero phase difference to be re-established. The periodicity of the function in Fig. 3A is again very evidently related to the spatial periodicity of the grating.

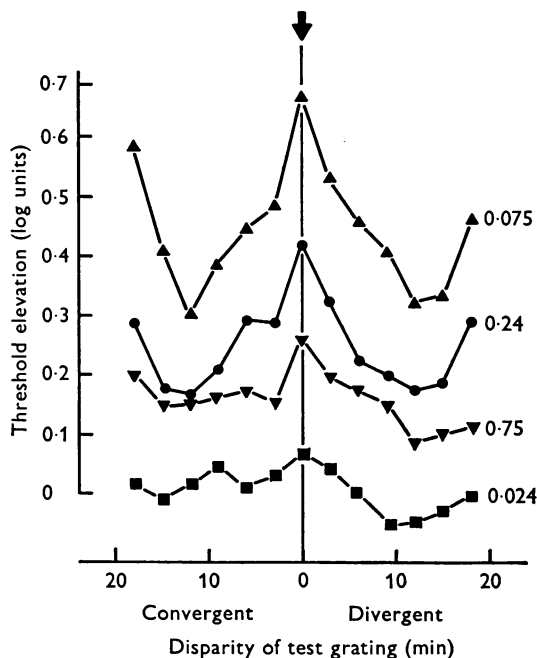


Fig. 4. Elevation of threshold for 2.5 c/deg gratings, after adapting to the same frequency at four different contrast levels: \blacktriangle 0.75, \bullet 0.24, \blacktriangledown 0.075, \blacksquare 0.024. Subject C.B.; $N = 4$.

The influence of adapting contrast. We repeated the experiment of Fig. 2 (but over a smaller range of disparity) and varied the contrast of the adapting grating. We used four different contrast levels (0.75, 0.24, 0.075 and 0.024), the last of which was only about 0.3 log units above contrast threshold for a grating of 2.5 c/deg. Fig. 4 shows the results, in the same way as in Figs. 2B and 3B, as the elevation of threshold.

Adapting to a disparity other than zero. We also asked the subject to adapt to a grating of 2.5 c/deg that he was *not* binocularly fixating. During adaptation the fixation line was displaced, by introducing a horizontal

constant d.c. shift to one of the lines, to a disparity of 12 min in front of the grating. So the adapting pattern was held constantly at a divergent absolute disparity of 12 min: hence the images were exactly in antiphase on the two retinae. When testing threshold the experimenter varied the disparity of the fixation line in the usual fashion but over a range centred on the disparity of adaptation. Fig. 5 has the results plotted as in Figs. 2*B* and 3*B* and clearly the function now peaks at the adapting disparity and not at zero disparity.

Adapting in one eye alone. Just to show that the variation of the after-effect with disparity is truly caused by adapting to a particular disparity, and was not merely an artifact of the testing situation, we tried adapting

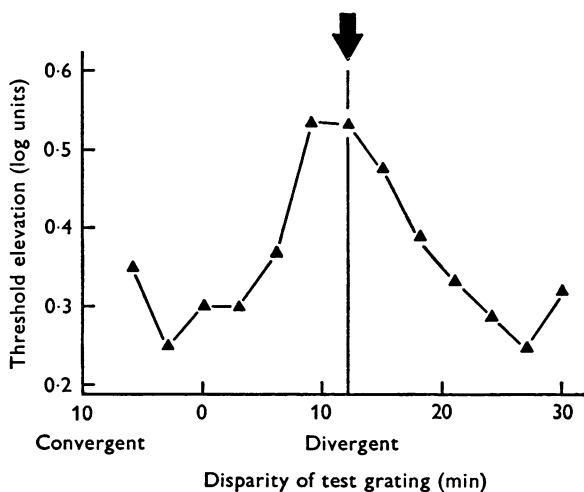


Fig. 5. Threshold elevation for gratings of 2.5 c/deg at various disparities, after adapting to a grating of the same frequency at a contrast of 0.7, and at a divergent (uncrossed) disparity of 12 min, shown by a filled arrow. Subject C.B.; $N = 4$.

in one eye alone and testing through both. Fig. 6 shows the results of an experiment, like that of Fig. 2, in which, however, the subject viewed the adapting grating of 2.5 c/deg with his right eye covered, and had both eyes open only during the testing situation. Now the elevation of threshold (Fig. 6*B*) is considerably less at all disparities and there is no detectable trend at all in the data.

Adapting to gratings: testing with a single bar

In these experiments the subject still had a grating to adapt to, but the pattern he set to threshold afterwards was not a grating but a single bright bar of square wave form, exactly in the middle of the screen. The width of

the bar was half the spatial period of the adapting grating, in other words the same thickness as a single bright bar in the adapting pattern. Antelman, Olson & Orbach (1969) have reported that adaptation to a grating can reduce the visibility of a single line, and Sullivan, Georgeson & Oatley (1972) showed that the elevation of threshold for a single bar of any width is greatest after adapting to gratings of low spatial frequency.

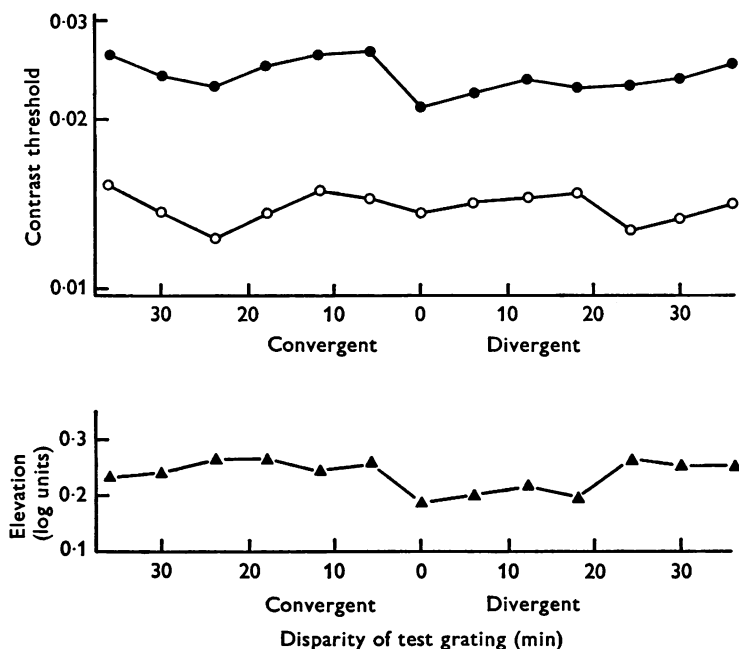


Fig. 6. An experiment to show that adaptation in one eye alone causes no disparity-specific elevation of threshold. The format is identical to that of Fig. 2, the spatial frequency was 2.5 c/deg and the adapting contrast 0.7. For all determinations of threshold, before (open circles) and after (filled circles) adapting, both eyes were open, but during adaptation the stimulus was only seen by the left eye. Subject C.B.; $N = 4$.

Fig. 7 has the results for an adapting grating of 2.5 c/deg, at a contrast of 0.7, and a test bar 12 min wide. The unadapted settings, shown as open symbols, vary with the disparity of the bar, the threshold being lowest at zero disparity, when the single bar is binocularly fixated. This variation can be explained at least partly on a monocular basis, since introduction of any disparity shifts the bar on to the peripheral retina in both eyes. After adaptation, however, the threshold is clearly most elevated at zero disparity, and the difference curves plotted in Fig. 7B show a much less marked periodic variation than those in Fig. 2B. The over-all effect is greater for one subject than the other, and we can suggest no simple

explanation for this discrepancy, but again the functions are very similar in general shape.

We repeated the experiment using an adapting grating of 5 c/deg and a test bar 6 min wide: Fig. 8 shows the results and once again the maximum threshold elevation is at the adapting disparity with only slight perturbations on the function at disparities equal to the spatial period of the grating (± 12 min).

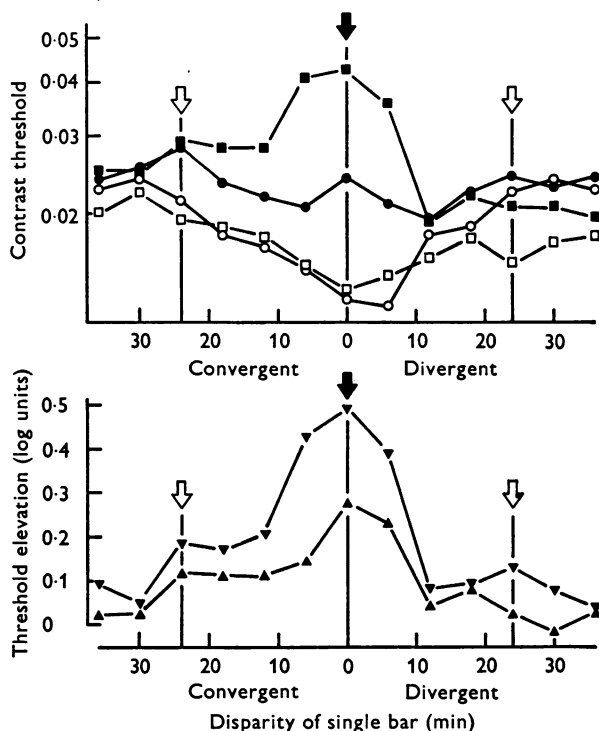


Fig. 7. Here the two subjects set their contrast thresholds for a single bright bar, 12 min wide at various disparities, before and after adapting to a grating of 2.5 c/deg, at a contrast of 0.7, in the same plane as the fixation line. Again, as in Fig. 2, the open arrows mark the disparities of ± 24 min, logically equivalent to zero disparity for a 2.5 c/deg grating. The symbols are exactly the same as in Fig. 2. $N = 8$ for C.B.; $N = 4$ for D.T.

The influence of adaptation on the apparent depth of other gratings

Blakemore & Sutton (1969) have argued that there are at least four possible classes of after-effect that might be generated by the prolonged stimulation of a particular sensory channel. Class 2 after-effects involve an increase in the detection threshold for the stimulus in question, so the after-effects reported so far in this paper are obviously of this class. However, there is another type of after-effect, class 4, predictable from a class 2 effect.

If adaptation reduces the sensitivity of a limited subset of detectors from a population of channels handling a particular sensory dimension, then the appearance of stimuli within the same submodality, but of different value from the adapting stimulus, should be altered. Stimuli should seem more different from the adapting stimulus than they really are. There are many

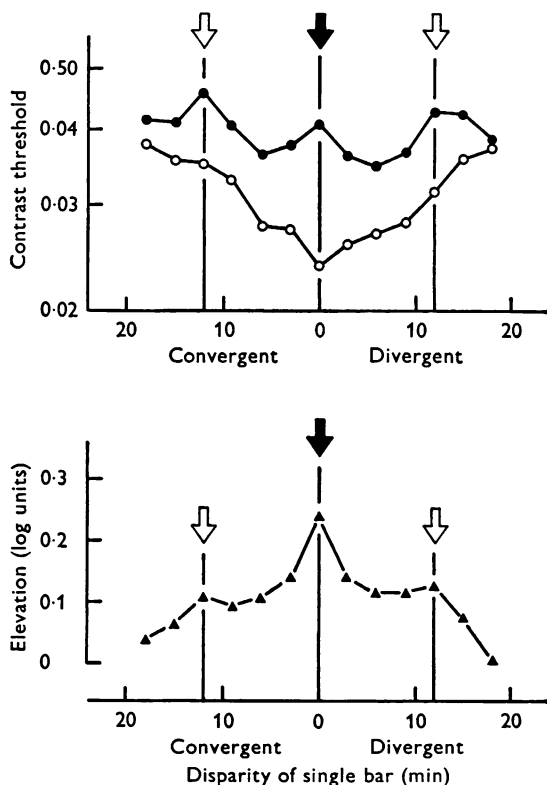


Fig. 8. This experiment was just like that for Fig. 7, but the bar was 6 min wide and the adapting grating was 5 c/deg. Subject C.B.; $N = 8$.

examples of class 4 after-effect, for example, Gibson's (1933) tilt after-effect, the figural after-effects of Köhler & Wallach (1944) and the perceived spatial frequency shift described by Blakemore, Nachmias & Sutton (1970). Köhler & Emery (1947) discovered such an after-effect within the disparity submodality and Blakemore & Julesz (1971) confirmed this observation using random-dot stereograms as their stimuli, and so refuting any criticism that the phenomenon could be explained at a monocular level. They found that adapting to a pattern at one distance from the fixation point makes a closer pattern look closer still and a more distant pattern look even further away.

We decided to look for such an after-effect using a grating as the adapting stimulus and we found that it does exist. First, we determined the frequency-of-seeing curve for the apparent depth of gratings over a small range of disparity around zero. We set the fixation line to a particular disparity and at the same time exposed a 2.5 c/deg grating, with a contrast of 0.2, on the display oscilloscope for about 2 sec. The subject had to say whether the grating seemed to be closer or more distant than the fixation line. The screen went blank and the fixation line returned to the plane of the

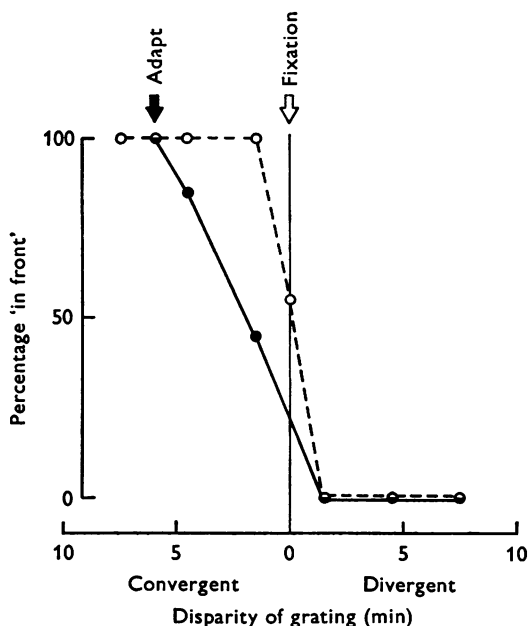


Fig. 9. Gratings of 2.5 c/deg, 0.2 contrast, were exposed for 2 sec each at various disparities close to fixation, before (open circles) and after (solid circles) adapting to a grating of 2.5 c/deg, 0.7 contrast, at a convergent disparity of 6 min, marked with a filled arrow. After adaptation, gratings between the adapting disparity and the fixation line (open arrow) were often reported as appearing to be behind fixation. Subject C.B.; $N = 20$.

screen in between settings. Altogether we took twenty judgements at each disparity and they were shown in random sequence. The results are shown as open circles in Fig. 9 and not surprisingly the curve is symmetric about zero disparity.

Now we repeated the whole procedure but for 3 min initially and for 15 sec between readings the fixation line moved back and forth behind the plane of an adapting grating of 2.5 c/deg at a contrast of 0.7. This grating was at a convergent disparity of 6 min, shown as a solid arrow in Fig. 9.

The judgements of depth for test gratings shown at various disparities during adaptation are plotted as filled circles: it is obvious that the apparent depth of gratings between the adapting grating and the fixation point was apparently displaced a little further away, so much so that they often elicited judgements of 'behind the fixation line'.

DISCUSSION

We assume that the selective elevation of threshold for a certain subclass of stimuli, after adaptation, implies that the range of stimuli in question is subdivided into a population of neural channels, each selectively sensitive to a different part of the range. We believe, therefore, that our results indicate that there are 'disparity-detectors' in the human brain, each tuned to a range of disparity much narrower than the total variation that we are capable of handling and discriminating (Blakemore, 1970*b*). In every case, adapting to a grating at a particular disparity causes a greater increase in contrast threshold for stimuli of very similar disparity than for those further removed in disparity.

This notion of disparity-selective channels is also supported by Blakemore & Julesz's (1971) experiment showing that adaptation to one depth plane can cause an apparent displacement in depth of a plane at another disparity. We have noticed the same perceptual distortion using gratings as the stimuli (Fig. 9), and D. E. Mitchell (in preparation) has explored this class 4 after-effect in detail. His results in every way parallel ours, for he finds that adapting to a grating causes a shift in the apparent disparity of gratings or single bars not in the same depth plane (or a logically equivalent plane) as that of the adapting grating.

Felton, Richards & Smith (1972) have also recently reported that adapting to a disparate grating influences the threshold of a grating in the same depth plane much more than that of a grating at the fixation point. Moreover, they also found that this difference in threshold elevation is strongest when the spatial period of the grating is half the disparity, thus setting the grating at antiphase on the two retinae during adaptation, as in our Fig. 5. Our results, taken together with the complementary evidence from these two other groups of workers, all add up to a powerful body of argument in favour of disparity-selective neurones in the human brain.

Now we should dispel a couple of possible methodological objections to our basic findings. One could argue that the reduced after-effect for test stimuli that are not being directly fixated is due to the longer time that such settings might take, because of their difficulty. If the settings took much longer than for directly fixated patterns the subject might have recovered considerably from the after-effect, since the strong initial effect

decays quite quickly. However, we noticed no difference in the length of time taken for different settings, and anyway this argument cannot cope with the selective elevation of threshold for a disparate pattern (shown in Fig. 5), nor with the lack of disparity-specific elevation after monocular adaptation (Fig. 6). A second possible objection to the measurements is that a change in convergence angle causes a change in the apparent size of the test targets, through the operation of 'zooming' (Richards, 1967). It is known that the threshold elevation effect only applies to stimuli of similar dimensions to the adapting pattern, so if the neural mechanism responsible for the change in apparent size operates before the point at which adaptation occurs, test stimuli of the wrong disparity would not be handled by the channel tuned to the spatial frequency of the adapting grating. But this argument cannot explain the periodic function measured with a grating as the test target, nor the uniform effect after monocular adaptation (Fig. 6), and, in any case, Blakemore, Garner and Sweet (1972) have found that size constancy does not operate before the site of the threshold elevation.

We were very interested in the precise reason for the periodic nature of the elevation caused by adapting and testing with repetitive patterns (Figs. 2*B*, 3*B*). There are at least two possible hypotheses, both of which depend on the fact that a grating is a logically ambiguous stimulus as far as disparity is concerned. Except for the cues provided by the edges of the pattern and any other non-repetitive features, a grating viewed binocularly can logically represent a surface at any one of an infinite number of depth planes at disparities equal to integral multiples of the spatial period of the grating. When the eyes converge or diverge over a grating it regularly fuses and again seems to be in the same frontoparallel plane as the fixation point for every increment of convergence equal to the period of the pattern. So one could propose that when the subject fixates the grating he is not only adapting neurones tuned to zero disparity but also those tuned to the other logical depth planes represented by the grating, even though the grating never appears to be located anywhere but at the fixation point. The threshold should then be elevated for stimuli at those disparities as well as at zero disparity. Alternatively, one could propose that only the zero disparity detectors are adapted, but that the *test* grating is detected by these adapted detectors whenever the convergence position brings it back into the same phase on the two retinae.

Under one hypothesis the cyclical function is due to the periodic nature of the adapting pattern, under the other one it is due to the periodicity of the test pattern. We used single bars as test stimuli to try to distinguish between these hypotheses but the answer is hardly unequivocal. Figs. 7*B* and 8*B* show that although there is certainly no periodicity of regular

amplitude in the elevation function for a single line, there is a hint of extra elevation at the logically equivalent depth planes on each side of the adapting disparity (± 24 min for Fig. 7 and ± 12 min for Fig. 8). So the adapting pattern influences almost exclusively those channels tuned to the depth plane at which it appears to be localized and much less those representing the logically equivalent depth planes. How this segregation of the adapting signal mainly into one set of disparity detectors is achieved is not obvious.

The narrowness of the tuning properties of human disparity-selective channels is a question of considerable interest and even though the precise nature of the adapting process is obscure the shape of the elevation function must bear some relationship to the tuning of individual channels. The functions shown in Figs. 7*B* and 8*B* are probably the most relevant to this question and their half-widths at half-amplitude are less than 10 min of disparity. This sort of value bears no comparison with the 10 sec of disparity or less needed for binocular depth discrimination, so clearly if the channels are this broadly tuned there must be some way in which the *relative* activity in different channels is judged in order to estimate the precise disparity of a stimulus.

It is interesting to compare the narrowness of these adaptation functions with the tuning properties of disparity-selective neurones in the cat cortex (Pettigrew *et al.* 1968; Joshua & Bishop, 1970). In fact the curves of Figs. 7*C* and 8*B* are not at all unlike some of the tuning curves for the cat's binocular neurones.

We should also consider any possible differences in tuning for different disparity channels. First compare Figs. 2*B* and 3*B*, the first for gratings of 2.5 c/deg and the second for 5 c/deg. Despite the complication of the periodicity of the functions it seems as though the tuning is narrower for 5 c/deg. This difference between the two frequencies is also evident in Figs. 7 and 8. Comparison between the uppermost curve in Fig. 4 and the function in Fig. 5, however, shows little difference in the tuning of detectors maximally sensitive to zero disparity and those most sensitive to a divergent disparity of 12 min. Even though these disparity sensitive channels are quite broad by comparison with the threshold of stereoscopic vision, they are themselves covering only a tiny fraction of the total range of disparity that man can discriminate (Blakemore, 1970*b*). Richards (1970) proposes that there are 'pools' of disparity analysers, perhaps receiving information from narrowly tuned detectors. These pools might be used for simple discriminations of whether an object is closer or more distant than the fixation point, or in the same plane as it.

So, all in all, we have used spatial adaptation to demonstrate neural mechanisms in man selectively sensitive to retinal disparity. It is already

known that adaptation to a grating causes an after-effect specific for the orientation and spatial frequency of the grating. Now we must add disparity to the list of contingent conditions necessary for optimal stimulation of the channels involved. Naturally it is tempting to compare this fascinating perceptual phenomenon with orientation detectors in the cat cortex that are also selective for the bar width and disparity of the stimulus.

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